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Plant Productivity and Nutrient Interrelationships of Perennials in the Mohave Desert

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ABSTRACT

Various studies of aspects of perennial plant productivity, most of which relate to carbon budget of the northern Mohave Desert, were continued in 1976. *Larrea tridentata* exposed to $^{14}CO_2$ in photosynthesis 26 months previously still retained about 20% of its ^{14}C and this was also the retention level at 16 months. However, lower specific activity was present in leaves at 26 months than at 16 months. A smaller percentage of ^{14}C in the plant also occurred in leaves at 26 months than at 16 months (3% vs. 10%). This indicates some, but little, reuse of carbon from the structural components of the plants. The strong tendency of the species to retain this carbon by conservation may be related to a survival mechanism. The specific activity of ^{14}C in the organic debris fraction from saturated salt flotation of roots after small and fine roots had been removed indicated that from 27 to 35% of the organic debris had the same specific activity as roots and could probably be considered as roots. This compares with the 45% value determined previously by a different technique. The below-ground:above-ground ratio for biomass of these plants was about 2.5:1. The ratio for the ^{14}C was about 1.4:1. The data obtained in this study were further used to correct our previous data for below-ground biomass. Somewhere between 3000 and 5000 kg roots/ha are present in the Rock Valley area. An increase with time of the below-ground:above-ground ^{14}C ratio probably indicates loss of ^{14}C from above-ground parts rather than additional transport to roots. Depth distribution of very fine roots at Rock Valley for 0-10, 10-20 and 20-30 cm were about 17, 42 and 41%, respectively. On April 22, there were 255 kg roots/ha from winter annuals in the Rock Valley area; 19% of them were in the first 5 cm of soil in contrast to 8% for 10 cm of soil for perennials. On Pahute Mesa of the Nevada Test Site in *Artemisia tridentata*, 8% of the roots were in the first 5 cm, indicating shallower rooting compared with the northern Mohave Desert. In a 12-week study of *Ambrosia dumosa*, in solution culture so that root behavior could be observed, plants increased in size over 17 times and flowered and produced seeds. The plants had received $^{14}CO_2$ in photosynthesis at the start. The gradual loss of ^{14}C in the 12 weeks averaged 3.5% per week (coefficient of variation = 58%). This represents an average respiration rate of 0.21 $mg \cdot C \cdot g$ dry $wt^{-1} \cdot hr^{-1}$. This compares favorably with other means for determination of respiration rate. The root portion of the plant, both as biomass and ^{14}C, varied little over the six sampling periods. The ^{14}C entering fruits and seeds came from leaves only, but fruit parts resulted more from new photosynthate than from retranslocation from leaves. In a study in which *A. dumosa* plants were defoliated, little ^{14}C moved from roots to new growth, as implied in the other study. The respiration rates found for desert soils were much lower than those from areas receiving high soil moisture. From 0 to about 5% of stems of different shrub species died in the year of study. Flower-bud removal from *Larrea tridentata* had no effect on growth characteristics of the shrubs in the year of study.

INTRODUCTION

One difficult aspect of plant studies in deserts is that of estimating their below-ground biomass. Our previous studies have emphasized the magnitude of this problem (Bamberg et al. 1973, 1974b; Vollmer et al. 1975, 1976; Wallace et al., in press; Wallace et al. 1974), and it is further emphasized by the wide differences in below-ground biomass reported for the same area by different workers within our own group.

Some approximations for root:shoot ratios in our studies for the northern Mohave Desert are near 1:1 while others are near 4:1. In the Great Basin Desert, root:shoot ratios are reported from around 8:1 to over 12:1 (Caldwell and Camp 1974; Caldwell et al. 1974; Caldwell et al. 1976). The purpose of this study was to further assess the problem of root biomass and to additionally study physiological aspects of roots of desert plants.

Several pieces of information were needed to construct a carbon budget for the ecosystem under study. The work done during this phase of the study was largely to provide such information.

OBJECTIVES

The specific objectives for the year were as follows:

1. Determine actual soil respiration rates for the Rock Valley study area and adjacent areas as applicable.
2. Determine long-time effects with the use of $^{14}CO_2$ on respiration and translocation of carbon in perennial desert plants.
3. Gain a better understanding of below-ground dynamics for plants in the northern Mohave Desert.
4. Determine rate and timing of stem death in perennial plants in the northern Mohave Desert.
5. Determine rate of stem growth in perennial desert plants.
6. Synthesize some of the data for the previous five years of study.

METHODS

^{14}C and Below-Ground Dynamics

Perennial plants in Mercury Valley, Nevada were exposed to $^{14}CO_2$ with the technique previously used in these studies (Bamberg et al. 1973, 1974b; Wallace et al. 1974).

Six naturally growing *Larrea tridentata* were exposed to $^{14}CO_2$ for 2 hr on the morning of May 14, 1974. Twigs were sampled at the end of this 2-hr period for use in estimating the total $^{14}CO_2$ fixed by the plants. Two of these plants were excavated 16 months later on September 17, 1975 (Vollmer et al. 1975). All parts were then analyzed for ^{14}C content by methods reported previously (Bamberg et al. 1973; Wallace et al., in press). Two other of these plants were sampled on July 16, 1976.

Soil from a 2.5-canopy sized area around the plants was sampled for use in fine-root biomass determinations. Soil samples (1 liter) were added to a saturated $MgSO_4$ solution. Soil organic matter was separated by flotation and hand-sorted to obtain fine roots. These roots were prepared and counted for ^{14}C. The roots were dried and ashed and found to contain 60-75% noncombustible ash. This high ash content was due to soil and salt contaminants adhering to roots. Root weights were normalized to 25% ash. In about 90% of the cases the fine roots contained ^{14}C, while only 10% of the organic debris samples contained the isotope. The amount of roots in the soil surrounding the plants was estimated by extrapolating from small soil samples to the total volume of soils within the area encompassed by 2.5 canopies to a depth of 30 cm. This method is similar to that employed by Bamberg et al. (1974b) and Vollmer et al. (1975).

Fine-Root Sampling

In April and September 1976, at the Nevada Test Site, a series of soil samples, 1 liter in volume each, were collected on the patterns for samples used by Bamberg et al. (1974a). The purpose was to evaluate the fine roots and organic debris floated with conventional salts so that our previous estimates for root biomass could be amended.

^{14}C Translocation

Two-month-old *Ambrosia dumosa* cuttings growing in 3700-ml nutrient solutions in a glasshouse were exposed to $^{14}CO_2$ by the general procedures previously used above. Three plants were separated into plant parts for ^{14}C determination after 24 hr, 1, 2, 4, 8 and 12 weeks to determine changes in distribution with time.

In order to ascertain movement of previously fixed ^{14}C from crown and root materials to shoots, an experiment was conducted in which four *A. dumosa* plants, each growing in 1600 g soil, were exposed to $^{14}CO_2$ as above. Leaves of the plants were sampled at 2, 24 and 48 hr; the shoots of the plants were cut off. The shoots were allowed to regrow and at 78 days the plants were removed from the soil and separated into parts, including fine roots separated out with concentrated $MgSO_4$. All plant parts were counted for ^{14}C.

Soil Respiration

Soil samples were collected during March-June 1976 in Rock Valley from four depths (5, 15, 25 and 35 cm). Samples were taken from bare areas and under *Larrea tridentata* and *Ambrosia dumosa* canopies.

Soil was then brought to the laboratory and passed through a 2-mm sieve. Approximately 400 cc of sieved soil were placed in each respiration jar. Three jars per depth per site were used: one control and two experimentals. One covered respiration jar from each depth was then autoclaved at 15-20 psi for 20 min and then allowed to cool. A dish with 10 ml of 1.0 N KOH was placed in each respiration jar and the jars sealed. After 24 hr the KOH was removed and placed in airtight vials to await titration.

The soil samples were weighed, oven-dried and reweighed. Water content was then calculated. The potassium hydroxide from each jar was divided into two 4-ml aliquots and phenolphthalein indicator and excess saturated $BaCl_2$ added. Titration to end point was made with 0.25 N HCl.

Carbon dioxide evolution was calculated with the use of the formula:

$$\text{mg } CO_2 = (B - V)\, NE$$

where V = ml of acid to titrate samples; B = ml of acid to titrate controls; N = normality of acid; E = equivalent weight of CO_2.

These methods were adapted from Stotzky (1965) and the data are stored under DSCODE A3UBD27.

Shrub Branch Death

In June 1975, the standing dead wood was removed from 10 *Larrea tridentata* and 10 *Krameria parvifolia* growing in Rock Valley. All live branches emanating from the base were counted. This procedure was repeated in April 1976 with 10 *Lycium andersonii*, 10 *Krameria parvifolia* and 10 more *Larrea* (A3UBD32).

Also, in April 1976 the number of dead branches on the first set of *Larrea* were counted and tagged. The *Krameria* were not sampled at this time since they had not yet broken dormancy and it was difficult to tell the difference between live and dead branches. Counts of dead branches were made on all plants in June 1976 and again in October 1976 after shrubs had responded to late summer-early fall rains (A3UBD32).

Additional information on death of woody plant parts was also obtained from the *Larrea* growth study (A3UBD31). Shoot tips, usually 1.5-2.0 cm in length, and stems, the last 10-15 cm of a branch, were tagged and followed from April 1976 to March 1977. Shoots and stems were checked at irregular intervals. Since no significant differences were noted between the controls and experimentals (see *Larrea* growth section), all data were lumped for this analysis. Replacement stems and shoots were made at various sampling dates in an attempt to maintain a constant sample size.

Larrea Growth

In April 1976, an experiment designed to study the effect of the reproductive effort on vegetative growth in *Larrea tridentata* was initiated (A3UBD31). Thirty *Larrea* plants growing in Plot 15 of the Rock Valley Validation Site were selected for study. Four branches per plant were permanently tagged. One shoot per branch was chosen for detailed growth measurements. Plants were examined about every two weeks throughout the reproductive season and at irregular intervals during the summer and fall.

The following measurements were made for all branches at each sampling period: numbers of shoot tips, flower buds, flowers and fruits. Individual shoot measurements consisted of: main shoot length and numbers of shoot laterals, main shoot nodes, lateral nodes and reproductive structures. After these measurements were taken, all the reproductive structures were removed from 20 experimental plants, while the reproductive organs on 10 controls were allowed to continue their development.

While measurements were made into December, the data reported here only include measurements from April to August due to time limitations for data processing. A second flush of growth occurred in September and October in response to late summer rains. This growth was almost entirely vegetative and, as a result, was not expected to be affected by our experimental manipulations.

Data were analyzed with the use of a group comparison test.

Table 1. Plant biomass and ^{14}C content of two *Larrea tridentata* plants within a 2.5-canopy area on 16 Jul, 1976. Plants exposed to $^{14}CO_2$ 26 mo previously at Mercury, Nevada and roots normalized to 25% ash

	Biomass (dry wt)			
	Plant #2		Plant #6	
	g	%	g	%
Flowers	5.5	1.0	5.1	0.8
Leaves	37.7	6.7	49.8	8.0
Stems	88.1	15.7	138.8	22.2
Roots	333.3	59.4	320.1	51.1
Organic debris[a]	355.8	--	275.9	--
Corrected value[b]	96.7	17.2	111.8	17.9
Total roots	430.0	76.6	431.9	69.0
Total	561.3	100.0	625.6	100

	^{14}C content					
	Plant #2			Plant #6		
	cpm	%	cpm/ g D.W.	cpm	%	cpm/ g D.W.
14 May, 1974	2,793,000	--	--	3,775,000	--	--
16 Jul, 1976	595,200	100.0	120	701,500	100.0	1,121
Flowers	665	0.1	120	510	0.1	100
Leaves	15,000	2.5	398	22,900	3.3	460
Stems	201,500	33.9	2,287	325,300	46.3	2,344
Roots	293,000	49.2	879	261,500	37.3	817
Organic debris[a]	85,000	14.3	239	91,300	13.0	331
Corrected value[b]	378,000	63.5	879	91,300	13.0	817
Total roots	378,000	63.5	879	352,800	56.3	817

[a]Organic material floated from soil with concentrated NaCl + normalized to 25% ash. Some of it may be a very fine fraction of roots.

[b]Organic debris corrected to specific activity of roots.

RESULTS AND DISCUSSION

^{14}C and Below-Ground Dynamics

Larrea tridentata, exposed to $^{14}CO_2$ 26 months previously at the Nevada Test Site, retained about 20% of the ^{14}C that was originally fixed (Table 1). This value was essentially unchanged from the 16 month value (Vollmer et al. 1976). A reevaluated set of the values at 16 months is in Table 2. At 26 months, however, a lower specific activity was found in leaves than at 16 months and a smaller percentage of the remaining ^{14}C was in the leaves at 26 months (3%) compared with 16 months (about 10%). This is indicative of low respiratory turnover and low remobilization of carbon from the structural components of this desert shrub.

Even though *L. tridentata* is evergreen, it loses its leaves, essentially on an annual basis (Wallace and Romney 1972), so there would be an annual loss of ^{14}C in an experiment such as this. The loss would not be as great as the ^{14}C content of leaves, however, because of the retranslocation of around 50% of the carbon from the leaves to the shrub before leaf abscission (Wallace et al., in press). Except for leaves, we were unable to distinguish between the ^{14}C contents of the two sets of plants collected at 16 months and at 26 months, respectively. Three annual phenological cycles are involved for the pair of plants harvested at 26 months. Somewhere around 20% of the original fixed ^{14}C was retained by the plants, and since this value was hardly changed, if at all, compared with 16 months, a survival mechanism may be involved. A high degree of conservation of carbon occurred. Another pair of plants originally exposed to $^{14}CO_2$ in May 1974 remains for a sampling at approximately 38 months.

The information in Tables 1 and 2 has bearing on the below-ground:above-ground ratio of biomass (Wallace et al., in press) and annual below-ground productivity of shrubs. Workers from the Great Basin Desert have found larger proportions of roots than we have for the Mohave Desert (Caldwell and Camp 1974; Caldwell et al. 1974; Caldwell et al. 1976). Our original estimates of below-ground:above-ground ratios were low, around 1 (Wallace et al. 1974). More recent estimates for the Mohave Desert are around 2 or 3 (Vollmer et al. 1976; Bamberg et al. 1974).

The biomass root:stem ratios for the two plants in Table 1 were 4.9 and 3.1; for ^{14}C the ratios were 1.9 and 1.2, months after labeling) were 1.7 and 3.9 for biomass and 0.6 and 0.8 for ^{14}C. It appeared that the biomass ratio was much higher at 26 months than at 16 months and that the ^{14}C ratio was much higher at 26 months than at 16 months. Part of the difference, however, could be due to technique. Part, however may be due to loss of ^{14}C from above-ground parts with age.

Table 2. Plant biomass and ^{14}C content within a 2.5-canopy area on 17 Sep, 1975 for two previously tagged (16 mo) *Larrea tridentata*

	Biomass (dry wt)			
	Plant #1		Plant #4	
	g	%	g	%
Small roots (< 1 mm)	52.1	--	80.1	--
Medium roots (1-3 mm)	109.0	--	164.0	--
Other roots	43.4	--	52.4	--
Total roots	204.5	52	296.5	61
Total roots corrected for organic debris	245.4	62	355.8	73
Stems	118.5	30	90.9	19
Leaves	30.3	8	38.2	8
Total	394.2	100	484.9	100

	^{14}C content					
	Plant #1			Plant #4		
	cpm	%	cpm/g D.W.	cpm	%	cpm/g D.W.
May 1974	1,583,000	--	--	3,200,000	--	--
Sep 1975	283,300	100	751	481,700	100	1,054
Roots	91,500	32	447	165,100	34	557
Total roots corrected for organic debris	109,700	39	447	198,200	41	557
Stems	150,500	53	1,270	211,400	44	2,326
Leaves	23,100	8	762	72,100	15	1,887

The data in Table 1 further resolve the problem of whether the organic debris floated from the soil samples with saturated solutions of salts should be considered as roots. Three factors relate to the problem. Such material is very high in ash because of the saturated salt and the soil contamination. Correction values are necessary. Not all subsamples from soil around ^{14}C-treated plants have ^{14}C in the organic debris floated from the soil samples, and these should probably not be considered as root material. The specific activity of the ^{14}C in the organic debris is lower than that for roots (Tables 1 and 2).

Nonroot material then is involved in correction of weights to a constant specific activity as was done in Tables 1 and 2. This could be erroneous because the ^{14}C could arise from dead, partially decayed roots.

The proportion of the organic debris not considered as roots was 73 and 65%, respectively for the two shrubs in Table 1. Vollmer et al. (1975) had determined that 45% of the organic debris was roots. The results of the two studies do not differ greatly.

The ratio of weight of roots to above-ground parts in Tables 1 and 2 varies from about 1.6 to over 3 with the corrected values for roots. The average of all four cases is 2.5. The ratio of the distribution of ^{14}C in the plants after the 26 months is also interesting (Table 1). The average value for the corrected root ^{14}C values is about 1.4. Neither the 2.5 nor the 1.4 ratios approach those found for Great Basin shrubs. They do, however, indicate the possible presence of greater biomass below-ground than above-ground.

Table 3. Estimates of standing stem and root weights from a 0.494-ha plot at Rock Valley. Revised from Wallace et al. (1974)

Species	No. of plants/ha	Stem dry wt (g/plant)	SD of stem wt (g/plant)	Stem kg/ha	Root kg/ha	Root[a] kg/ha	Root[b] kg/ha
Acamptopappus shockleyi	47	68.3	82.8	3.2	1.8	2.4	2.9
Atriplex confertifolia	75	33.7	32.8	2.5	1.1	1.5	1.8
Ephedra nevadensis	783	119.1	202.9	93.3	77.9	102.8	126.5
Ceratoides lanata	478	62.7	96.9	30.0	27.0	35.6	43.8
Ambrosia dumosa	2,394	108.7	111.0	260.2	301.0	397.3	488.7
Grayia spinosa	1,196	74.3	85.8	88.9	64.0	84.5	103.9
Krameria parvifolia	1,482	136.4	96.9	202.1	159.4	210.4	258.8
Larrea tridentata	1,046	437.9	454.1	458.0	566.7	748.0	920.1
Lycium andersonii	710	371.4	244.3	263.7	220.1	290.5	357.4
Lycium pallidum	459	264.4	216.4	121.3	199.7	263.6	324.3
Total	8,670	--	--	1,523.3	1,618.7	2,136.6	2,628.2

[a]Root corrected for debris (1.32).
[b]Root corrected for interspace (1.23).

In 1974, we made some estimates of root biomass for the northern Mohave Desert (Table 2 of Wallace et al. 1974). It would appear from the data in Table 1 of this report, that the root values probably should be further corrected for those in the 1974 report to include the root portion in the organic debris portion. An estimate of correction factor is the corrected vs. the uncorrected values in Table 1. These are 1.29 (430/333) and 1.35 (432/320) for weights of the two plants and the values in Table 2 (Wallace et al. 1974) should be corrected by that amount. An interspace correction should also be made in that the 1974 samples were extended into the interspace soil only as far as we found roots. The development of a correction factor of 1.23 for interspace is given below and the values are included in Table 3.

The twice-corrected values for root:stem in Table 3 is 1.73 and for root:root + stem is 0.63. These values are subject to errors, but still they are lower than similar data from the Great Basin Desert.

The root:stem ratio of 1.4 for ^{14}C from Table 1 is of interest. After 26 months, more of the ^{14}C in the plants is below-ground than above, corresponding with the root weights. In our earlier studies (Wallace and Romney, in press) the ^{14}C ratio for root:stem was around 1/5 for the relatively short-time basis. The shift may be related to loss of ^{14}C-containing materials from shoots rather than to the transport of more of it below-ground. This would indicate that, over a period of years, there is a greater loss of above-ground parts than below-ground parts.

Fine-Root Sampling

The sampling made in Rock Valley in 1976 using the technique of Bamberg et al. (1974a; Table 4) was

Table 4. Root sampling pattern of Bamberg et al. (1974a) in Rock Valley 22 Apr, 1976 in typical *Lycium pallidum* dominated area. Values expressed in kg/ha

	Interspace (80%)	In canopy (13.3%)	Under plant (6.7%)	Total (100%)
	0-10 cm			
Large roots	--	--	--	--
Small roots	--	--	--	--
Fine roots	10	3	3	16
Organic debris*	75	21	32	128
35% organic debris*	26	7	11	44
	10-20 cm			
Large roots	105	--	32	137
Small roots	54	--	3	57
Fine roots	30	11	11	52
Organic debris*	193	19	64	276
35% organic debris*	68	7	22	97
	20-30 cm			
Large roots	143	14	7	164
Small roots	38	7	5	50
Fine roots	30	4	9	43
Organic debris*	214	27	42	283
35% organic debris*	75	9	15	99
Total	891	106	208	1,204
Corrected total	579	62	118	759
	Total by depth			
0-10 cm	36	10	14	60
10-20 cm	257	18	68	343
20-30 cm	286	34	36	356

*Organic debris also normalized to 17% ash to correspond with roots in general from the northern Mohave Desert.

designed to sample those roots possibly missed in our technique of 1974 (Wallace et al. 1974). The main roots were not included in the sample. These involve the very fine roots, organic debris and the interspaces. Further study and modification of the technique of Bamberg et al. (1974a) were necessary because of the ash problem (contamination of fine roots and organic debris with soil, etc.) and because of the need to determine a fraction of the organic debris that could be assigned to the root fraction. The ^{14}C values indicated roughly 35% which was used as a correction factor in Table 4. The total amount of roots in the profile on a kg/ha basis (759) approximated the corrections made in Table 3.

Vollmer et al. (1976) gave corrections for below-ground: above-ground ratios (Table 4) of data presented in Vollmer et al. (1975, Table 10). The total below-ground biomass of 9466 for 1974 was too high. It was corrected to 4929 in 1976. There is probably little reason to further revise the value.

Depth distribution of the very fine roots was in kg/ha; 60, 149 and 142 for 0-10, 10-20 and 20-30 cm, respectively (Table 4). This was not different from roots in general. The surface soils of the northern Mohave Desert are low in both large and fine roots and this may be related to high soil surface temperatures and low soil moisture of the summer months. This condition (few perennial roots on the surface 10 cm) supports a relatively large number of winter annuals (Turner and McBrayer 1974).

Table 5. Root sampling pattern of Bamberg et al. (1974a) at Frenchman Flat, 22 Apr, 1976, in typical *Ambrosia dumosa* dominated area. Values expressed in kg/ha

	Interspace (80%)	In canopy (13.3%)	Under plant (6.7%)	Total (100%)
	0-10 cm			
Large roots (> 3 mm)	--	--	--	--
Small roots (1-3 mm)	--	--	--	--
Fine roots (< 1 mm)	--	--	--	--
Organic debris*	46	8	92	146
35% of organic debris*	16	3	32	51
	10-20 cm			
Large roots	--	--	--	--
Small roots	--	13	5	18
Fine roots	--	4	1	5
Organic debris*	121	22	31	174
35% of organic debris*	42	8	11	61
	20-30 cm			
Large roots	--	25	14	39
Small roots	--	5	2	6
Fine roots	18	17	1	36
Organic debris*	47	44	8	99
35% organic debris*	17	15	3	35
Total	232	138	154	524
Corrected total	93	90	69	252

*Organic debris also normalized to 17% ash to correspond with roots in general from the northern Mohave Desert.

Table 6. Root sampling pattern of Bamberg et al. (1974a) in Mercury, Nevada, 22 Apr, 1976 in typical *Lycium andersonii* dominated area

	Interspace	In canopy	Under plant	Total
	0-10 cm			
Large roots	--	--	21	21
Small roots	--	--	4	4
Fine roots	17	--	4	21
Organic debris*	50	33	249	332
35% organic debris*	18	12	87	117
	10-20 cm			
Large roots	--	--	9	9
Small roots	--	--	7	7
Fine roots	51	2	7	60
Organic debris*	239	13	136	338
35% organic debris*	84	5	48	137
	20-30 cm			
Large roots	--	25	457	482
Small roots	--	5	60	65
Fine roots	27	17	22	66
Organic debris*	152	44	215	411
35% organic debris*	53	15	75	143
Total	536	139	1,191	1,866
Corrected total	250	81	801	1,132

*Organic debris also normalized to 17% ash to correspond with roots in general from the northern Mohave Desert.

Soil samples were also taken for roots in Frenchman Flat and Mercury Valley using the above procedures of Bamberg et al. (1974a). Although the procedures were not designed to collect the large and intermediate roots, some appeared in the samples (Tables 5 and 6). There were 252 kg/ha for small and fine roots at the Frenchman Flat site and 1132 kg/ha for the Mercury Valley site. These samples were taken in spring so they should have shown a component of fine roots due to phenological stage.

Table 7. Depth distribution of roots from annual plants from the Nevada Test Site collected 22 Apr, 1976. Values expressed in kg/ha

	100% of area			20% of area		
	Mercury	Frenchman Flat	Rock Valley	Mercury	Frenchman Flat	Rock Valley
	0-5 cm depth					
Litter	870	367	--	--	--	--
Large roots	--	--	189	--	--	38
Small roots	--	--	25	--	--	5
Fine roots	--	--	24	--	--	5
Organic debris*	1,629	516	249	326	103	50
35% of organic debris*	570	181	87	114	36	18
	5-10 cm depth					
Large roots	--	--	--	--	--	--
Small roots	--	--	20	--	--	4
Fine roots	145	5	27	29	1	5
Organic debris*	691	68	218	138	18	44
35% of organic debris*	242	31	76	48	6	15
	10-20 cm depth					
Large roots	183	--	181	37	--	36
Small roots	196	109	62	39	22	12
Fine roots	227	53	42	45	11	8
Organic debris*	1,268	235	552	254	47	110
35% of organic debris*	444	82	193	99	16	39
	20-30 cm depth					
Large roots	146	--	--	29	--	--
Small roots	185	--	77	37	--	15
Fine roots	163	25	47	33	5	9
Organic debris*	1,461	298	651	292	60	130
35% of organic debris*	511	104	228	102	21	46
Total (– litter)	6,295	1,325	2,364	1,259	265	471
Corrected total	3,013	590	1,278	602	118	255
	Totals by depth					
0-5 cm	570	181	325	114	36	66
5-10 cm	387	36	123	77	7	24
10-20 cm	1,050	244	478	210	49	95
20-30 cm	1,006	129	352	201	26	70

*Organic debris also normalized to 17% ash to correspond with roots in general from the northern Mohave Desert.

Roots associated with winter annual plants are shown in Table 7. Two sets of values are shown. One is based on the assumption that the biomass is uniform and the other (realistic) is that the winter annuals occupy 20% of the land area. On this basis, the biomass estimates in kg/ha for winter annual roots were 602, 118 and 255 for Mercury Valley, Frenchman Flat and Rock Valley, respectively (April 22, 1976).

The depth distribution of the annual roots was more shallow than for perennial plants, as expected. The first 5 cm of soil had 19, 31 and 26%, respectively, for Mercury Valley, Frenchman Flat and Rock Valley. In the first 10 cm of soil from Rock Valley, only 8% of the roots (mostly fine) from this sampling were present (Table 4). In Frenchman Flat and Mercury Valley there were 20 and 14%, respectively, but these values are for 10 cm while those for annuals were for 5 cm.

Another set of samples of soil by the same procedure was taken on September 24, 1976 in a *Larrea tridentata-Ambrosia dumosa* community (Table 8). The value of 35% of organic debris as determined above with ^{14}C was used to correct the values for estimation of fine roots. The values were also normalized to 17% ash. The total root biomass in kg/ha was 797 at this September date, which is essentially the same as the April date in Table 4 (759 kg/ha). Both are acceptable estimates for the correction factor for the original estimate in Table 3.

Table 8. Roots in soil samples collected in *Larrea-Ambrosia* communities on 24 Sep, 1976. Values expressed in kg/ha

	Interspace (80%)	In canopy (13.3%)	Under plant (6.7%)	Total (100%)
	0-10 cm			
Large roots	--	--	--	--
Small roots	--	--	19	19
Fine roots	25	19	8	52
35% of organic debris*	19	18	81	118
	10-20 cm			
Large roots	--	--	--	--
Small roots	--	137	48	185
Fine roots	46	34	26	106
35% of organic debris*	16	8	43	67
	20-30 cm			
Large roots	--	23	42	65
Small roots	--	25	46	71
Fine roots	25	12	12	49
35% of organic debris*	15	5	45	65
Total	146	281	370	797

*Values normalized 17% ash and corrected to 35%.

Table 9. Root distribution in *Artemisia tridentata* on Pahute Mesa at the Nevada Test Site. Normalized to 17% ash

Depth (cm)	Under plant (kg/ha)	In canopy (kg/ha)	Interspace (kg/ha)	Total (kg/ha)	Distribution for 5-cm increments (%)
	Large roots (> 3 mm)				
0-5	--	--	--	--	0.0
5-10	93	56	260	409	13.7
10-20	590	260	--	850	14.3
	Small roots (1-3 mm)				
0-5	2	10	--	12	0.4
5-10	17	23	140	180	6.1
10-20	70	140	140	350	5.9
	Fine roots (< 1 mm)				
0-5	21	10	--	31	1.0
5-10	32	47	77	156	5.2
10-20	78	77	98	253	4.3
	35% of organic debris				
0-5	151	34	5	190	6.4
5-10	58	36	100	194	6.5
10-20	69	100	181	350	5.9
	Total				
0-5	174	54	5	233	7.8
5-10	200	162	577	939	31.6
10-20	807	577	419	1803	30.3
Total	1,181	793	1,001	2,975	100.0

In order to compare the root patterns of the first 5 cm of soil of the Great Basin Desert (an *Artemisia* community) with the northern Mohave Desert, a root sampling procedure as above was used at Pahute Mesa (Table 9) of the Nevada Test Site. The percentage of the roots in the first 5 cm was 7.8% which is about the same as in the first 10 cm of the northern Mohave Desert. In the first 10 cm at Pahute Mesa, 39% of the roots were present. Rock existed below 20 cm at the site sampled so no roots were at lower depths. The root sample of 2975 kg/ha compares with an estimated above-ground biomass of about 3000 kg/ha (Wallace et al. 1972).

Table 10. Dry wt and distribution of dry wt and ^{14}C in plant parts at different times following exposure of *Ambrosia dumosa* to $^{14}CO_2$

	24 hr	1 wk	2 wk	4 wk	8 wk	12 wk
	dry wt (mg/plant)					
Leaf	992	1,191	3,350	3,520	7,655	18,361
Stem	700	1,454	1,758	3,226	6,752	10,150
Transition	58	94	133	212	224	1,078
Root	190	397	576	890	2,304	2,555
Seed	--	--	--	2,023	2,673	1,816
Total	1,940	3,856	5,817	9,871	19,608	33,960
	cpm/g					
Leaf	553,267	274,933	163,347	109,760	41,950	18,990
Stem	338,980	124,540	109,673	61,447	20,240	17,910
Transition	72,695	62,120	91,013	34,860	26,020	16,780
Root	222,033	112,987	78,693	54,513	17,630	14,830
Seed	--	--	--	78,735	50,546	66,030
	cpm/plant					
Leaf	548,841	525,395	547,212	386,355	321,127	348,675
Stem	237,286	181,081	192,806	198,228	136,660	181,787
Transition	4,216	5,839	12,105	7,390	5,828	18,089
Root	42,186	44,856	45,327	48,516	40,620	37,891
Seed	--	--	--	78,735	50,546	66,030
Total	832,529	757,170	797,450	719,224	554,781	652,472
	dry wt/total plant wt (%)					
Leaf	51.1	49.6	57.6	35.7	39.0	54.0
Stem	36.1	37.7	30.2	32.7	34.5	29.9
Root	9.8	10.3	9.9	9.0	11.8	7.5
Transition	3.0	2.4	2.3	2.1	1.1	3.2
Seed	0.0	0.0	0.0	20.5	13.6	5.4
Total	100.0	100.0	100.0	100.0	100.0	100.0
	cpm/plant (%)					
Leaf	65.9	69.4	68.6	53.7	57.9	53.4
Stem	28.5	23.9	24.2	27.6	24.6	27.9
Transition	0.5	0.8	1.5	1.0	1.1	2.8
Root	5.1	5.9	5.7	6.8	7.3	5.8
Seed	0.0	0.0	0.0	10.9	9.1	10.1
Total	100.0	100.0	100.0	100.0	100.0	100.0

^{14}C Translocation

Redistribution or reallocation of carbon in *Ambrosia dumosa* was studied in a controlled experiment made in solution culture in a glasshouse (Table 10). Changes were followed over six different sampling times over a 12-week period. The plants flowered and fruited during the test, which permitted a measure of mobility of the carbon from the ^{14}C tagging time. Triplicate plants for each time period were used for the measurement.

The plants increased in size over 17 times during the course of the 12-week experiment. The respiratory loss of the ^{14}C was relatively little. The estimates are rough and were 9% at 1 week, 4% for 2 weeks, 14% for 4 weeks, 33% for 8 weeks and 22% for 12 weeks. The irregularity of the values indicate variability. A normalized value for all five values results in an average of 3.5% per week. A standard deviation for the 3.5% value is 2.07 with a coefficient variation of 58%.

If this value (3.5% per week) represents a respiration rate, it would be 2.1 x 10 (E — 4) mg C/hr — mg dry wt or 0.21 mg C · g dry wt^{-1} · hr^{-1} at any point in the history of these plants. This compares fairly well for actual respiration measurements. It represents the respiration rate for the active growing stages and not dormancy for this species (Vollmer et al. 1976).

Table 11. Distribution of ^{14}C in *Ambrosia dumosa* plants 78 days after exposure of the shoots to $^{14}CO_2$ and 76 days after removal of all the leaves and stems from the plants. Leaf concentration of ^{14}C at 2, 24 and 48 hr from exposure to $^{14}CO_2$ were 82,135; 39,670 and 37,230 cpm/g dry wt, respectively

Plant part	Dry wt	cpm/g	cpm/plant	%	SD of %	C.V. (%)
Leaves	2.02	610	1,232	8.0	2.50	31
New stem	0.53	135	72	0.5	0.07	13
Old stem	2.53	1,520	3,846	24.9	7.31	29
Crown	0.82	1,725	1,415	9.1	6.03	66
Large root	0.37	2,580	955	6.2	3.18	51
Small root	0.33	3,525	1,163	7.5	1.47	20
Fine root	1.82	3,730	6,789	43.8	11.78	27
Totals or means	8.42	1,838	15,472	100.0	--	--

The root portion of the plants varied little for the six sampling periods, even when seeds were produced. The percentage of total ^{14}C in roots was about the same at 24 hr (5.1%) as at 12 weeks (5.8%). The ^{14}C moved to roots only on the day of fixation. None left the roots thereafter during the 12 weeks of the test. More dry matter than ^{14}C was moved to the fruiting parts and seeds, implying that new photosynthate mostly was used for fruiting. The ^{14}C that was translocated to seeds seemed to come from leaves only.

Redistribution of carbon in *A. dumosa* was further studied with plants in soil in a glasshouse. Four plants exposed to $^{14}CO_2$ were defoliated after 2 days and a portion of the stem was also removed. Any ^{14}C found in leaves and new stems thereafter had to be translocated from old parts. After 78 days, 8% of the ^{14}C was in leaves, 0.5% in new stems with over 57% in roots (Table 11). This indicates, as in other studies, that ^{14}C is not readily moved after initial distribution. The ^{14}C in the leaves probably was mobilized when the leaves were initiated. At 78 days, 24% of the plant biomass was leaves with 8% of the ^{14}C. Thirty percent of the plant biomass was roots with 57.5% of the ^{14}C.

Leaf concentrations of ^{14}C at 2, 24 and 48 hr from exposure to $^{14}CO_2$ (82, 135, 39, 630 and 37,230) indicated that there was considerable loss due to dark respiration in the C3 plant, or that this was the time in which translocation to roots primarily occurred.

Soil Respiration

Soil respiration rates showed a large amount of variability in relation to soil water content, sample depth and collection data (Table 12). A summary of the significance of soil respiration-soil water regression analyses is presented in Table 13. Only the 25-cm *Ambrosia* sample and the 5-cm lumped sample showed significance. But due to the high variability and small sizes, not much importance is attached to this statistic. In addition, when respiration rates for all the samples of the same soil type (*Larrea*, *Ambrosia* or bare) were compared with each other, no significant differences were noted.

Table 12. Respiration rates (mg $CO_2 \cdot$ g dry wt soil$^{-1} \cdot$ 24 hr^{-1}) and percent moisture (in parentheses) for Rock Valley soil during 1976 (DSCODE A3UBD27)

Location/date	Depth (cm)			
	5	15	25	35
Bare soil				
3/29	0.015 (4.6)	0.044 (6.2)	0.021 (6.4)	0.011 (5.7)
4/19	0.057 (7.0)	0.011 (8.5)	0.028 (7.8)	0.027 (8.0)
5/4	0.044 (2.6)	0.107 (6.3)	0.075 (6.3)	0.056 (4.8)
5/17	0.040 (5.7)	0.079 (6.1)	0.125 (6.1)	0.038 (5.4)
6/16	-- (2.1)	0.021 (3.4)	0.023 (5.1)	-- (4.7)
Larrea				
3/30	0.043 (5.1)	0.023 (7.1)	0.031 (7.3)	0.018 (6.7)
4/19	0.033 (5.4)	0.032 (7.5)	0.015 (8.5)	0.023 (10.7)
5/4	0.045 (2.1)	0.055 (5.2)	0.095 (7.1)	0.080 (8.5)
5/17	0.006 (1.3)	0.000 (3.4)	0.023 (4.0)	0.024 (5.7)
6/16	0.029 (1.2)	0.014 (2.6)	0.000 (4.0)	0.010 (4.8)
Ambrosia				
3/31	0.025 (3.7)	0.011 (5.2)	0.017 (5.7)	0.027 (6.8)
4/20	0.048 (6.2)	0.040 (8.4)	0.031 (7.9)	0.028 (8.5)
5/5	0.006 (1.4)	0.021 (3.7)	0.014 (5.0)	0.027 (5.9)
5/18	0.024 (1.4)	0.042 (4.4)	0.026 (6.4)	0.028 (5.5)

Respiration rates of Rock Valley soil were compared with rates reported by Coleman (1973) for old-field and hardwood forest soils (Table 14). Desert soil respiration is low by comparison. During the peak of the growing season, the mean respiration rate of Rock Valley soil (5-cm depth) was only one-half of that found in old-field soil during the winter and only 10% of forest spring rates.

SHRUB BRANCH DEATH

The conversion "rates" of whole branches from the live to dead category at different times of the year for four shrub species are shown in Table 15. A considerable amount of variation existed between shrubs. In fact, no significant differences in percent branch death were noted at the intraspecific level. *Larrea* branch death was significantly ($P < 0.01$) lower than that of *Krameria* for the June 1975-June 1976 interval. The summer branch death rates (June 1976-October 1976) of *Lycium* and *Krameria* were also significantly different at the 99% confidence level.

Results of the *Larrea* stem and shoot death study are presented in Table 16. Very few stems died during the experiment and all of these losses occurred during the hot, dry summer months. Chi-square analysis revealed no significant differences at the 95% level in the shoot death rates for the various sampling intervals (Table 17). However, there is a strong trend toward lower than expected rates in the late spring and winter and higher rates in the summer and fall.

While the above stem and shoot death data for each sample interval were treated independently of each other, we also followed 120 tagged branches from April to August 1976. During this period, 2.5% of the stems and 10.8% of the shoots died.

Table 13. Significance of regression lines of soil respiration rates on soil water content. Sample number in parentheses. X: $P < 0.05$; O: $P > 0.05$

Soil type	Depth (cm)				
	5	15	25	35	All
Bare	(4) 0	(5) 0	(5) 0	(4) 0	(18) 0
Ambrosia	(4) 0	(4) 0	(4) X	(4) 0	(16) 0
Larrea	(5) 0	(5) 0	(5) 0	(5) 0	(20) 0
All	(13) X	(14) 0	(14) 0	(14) 0	(54) 0

Table 14. Comparison of respiration rates of surface soil (mg $CO_2 \cdot$ g dry wt$^{-1} \cdot$ 24 hr^{-1}) for desert, old-field and hardwood forest. Data from Coleman (1973)

Location	Month	Rates
Desert	Apr-Jun	0.032
Old-field	May	0.102
Old-field	Dec-Jan	0.065
Forest	Apr	0.290
Forest	Jun	0.316

Table 15. Branch death in four shrub species in Rock Valley (A3UBD32)

Species/time interval	N	Mean old live branches/shrub	Mean new dead branches/shrub	% death
Larrea				
06/26/75-04/05/76	10	14.1	0.0	0.0
06/26/75-06/28/76	10	14.1	0.4	2.8
04/05/76-06/28/76	20	17.7	0.4	2.3
06/28/76-10/08/76	20	17.3	0.4	2.3
Krameria				
06/16/75-06/28/76	10	28.4	1.1	3.9
06/28/76-10/08/76	10	27.3	2.0	7.3
Ambrosia				
04/05/76-06/28/76	10	23.6	0.3	1.3
06/28/76-10/08/76	10	23.3	1.4	6.0
Lycium				
04/05/76-06/28/76	10	29.8	0.0	0.0
06/28/76-10/08/76	10	29.8	0.7	2.3

Table 16. Stem and shoot death in *Larrea tridentata* in Rock Valley (A3UBD31)

Sampling interval	Days	N	Dead shoots	N	Dead stems
04/28-05/12	14	120	1	120	0
05/12-06/03	22	120	0	120	0
06/03-06/23	20	120	6	120	2
06/23-08/03	41	117	6	118	1
08/03-09/27	55	120	11	120	1
09/27-10/14	17	120	4	120	0
10/14-12/01	48	120	10	120	0
12/01-03/08	97	119	10	119	0

Table 17. Chi-square analysis of *Larrea* shoot death

Sample interval	Observed	Expected	
04/28-06/03	1.00	5.53	$X^2 = 8.15$
06/03-08/03	12.15	9.37	
08/03-09/27	11.00	8.45	Df = 4
09/27-12/01	14.00	9.98	
12/01-03/08	10.08	22.27	$0.1 > P > 0.05$

Table 18. Growth characteristics of control and experimental *Larrea tridentata* (A3UBD31)

Growth characteristics	Control (n = 40)		Experimental (n = 80)	
	$\bar{X}$	SE	$\bar{X}$	SE
Initial # of shoot tips per branch	36.3	2.4	35.1	1.5
Change in # of shoot tips per branch	4.4	1.4	6.2	1.3
# of flower buds per branch	7.7	1.2	8.9	1.1
# of fruit per branch	5.0	0.9	0.0	0.0
Change in shoot length (mm)	8.1	1.7	7.2	1.4
Change in lateral length (mm)	7.8	2.2	7.3	1.3
Change in # of shoot nodes	1.2	0.3	1.1	0.3
Change in # of lateral nodes	2.0	0.5	2.4	0.4
# of shoot reproductive organs	0.9	0.2	0.7	0.1

Larrea Growth

In *Larrea tridentata*, reproductive structures are formed at the younger nodes near the shoot tips. Since it is difficult to ascertain whether a given node is capable of producing a flower bud, it was felt that a count of the shoot tips on a branch could serve as the common denominator for the determination of reproductive success. No significant difference was noted in the initial numbers of branch shoot tips between controls and experimentals. Therefore, a direct comparison of the growth characteristics should be valid.

Despite the fact that the flower buds were not allowed to develop on the experimental plants, there were no significant differences between the controls and experimentals in the seven growth categories measured (Table 18). This negative response may be attributed to the relatively small amount of fruit produced in the controls. While 65% of the flower buds on the controls formed fruit, this only resulted in 14% of the shoot tips bearing fruit. It would not be expected that this poor reproductive effort would significantly limit the vegetative growth of *Larrea*.

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